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NEST SITE SELECTION IN A HOT DESERT: TRADE-OFF BETWEEN MICROCLIMATE AND PREDATION RISK?

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Abstract. Nest placement affects the risk of predation on both eggs and incubating parents and determines the microclimate for incubation, two functions that may be in conflict, especially in hot deserts. We studied the roles of microclimate and nest predation on nest site selection by Hoopoe Larks (*Alaemon alaudipes*) in the Arabian Desert. Hoopoe Larks build nests in three microsites: on the gravel plain away from vegetation, at the base of bushes, or above ground in bushes. Early in the breeding season, 70% of nests were placed on the ground, but as the season progressed, nests in small bushes represented 77% of total nests; nest cover increased from 5% to 21%. Daily survival rate of natural nests was 0.82. Predation on eggs did not differ among nest sites, either for natural nests or in an experiment with artificial nests. Measurements of operative and egg temperatures showed that artificial nests on the gravel plain experience higher temperatures than those under and in bushes. Nest attendance totaled 77% of daytime in nests under bushes and 81% in nests in or on top of bushes, with the larger share of attendance contributed by females. However, during midday, when evaporative water requirements—estimated from temperature profiles at artificial nests—were 10–15-fold higher than during early morning, males and females shared incubation duties almost equally. We hypothesize that Hoopoe Larks favor exposed nest sites to reduce predation risk to themselves as incubating parents, but as the season progresses, they select nest sites with more cover at the base of or within bushes because the thermal environment forces them to do so.

Key words: Alaemon alaudipes*, desert, egg temperature, Hoopoe Lark, incubation, microclimate, nest predation.*

Selección de Sitios de Nidificación en un Desierto Cálido: ¿Un Compromiso entre el Microclima y el Riesgo de Depredación?

Resumen. La ubicación de los nidos afecta el riesgo de depredación de los huevos y de los parentales incubantes, así como el microclima de la incubación. Estas dos funciones pueden estar en conflicto, especialmente en desiertos cálidos. Estudiamos el papel del microclima y de la depredación de los nidos sobre la selección de sitios de nidificación por parte de *Alaemon alaudipes* en el desierto de Arabia. Esta especie construye nidos en tres micrositios: planicies de gravilla lejos de la vegetación, la base de los arbustos, o arbustos por encima del suelo. En la parte inicial de la época reproductiva, el 70% de los nidos estuvieron ubicados en el suelo, pero a medida que transcurrió la estación, los nidos ubicados en pequeños arbustos representaron el 77% del total y la cobertura de los nidos se incrementó del 5% al 21%. La tasa de supervivencia diaria de los nidos fue de 0.82. La depredación sobre los huevos no difirió entre los sitios de nidificación para nidos naturales ni para los nidos artificiales de un experimento. Las mediciones de las temperaturas operativas y de los huevos mostraron que los nidos artificiales ubicados en la planicie de gravilla están expuestos a temperaturas mayores que los nidos ubicados bajo arbustos y sobre éstos. Los parentales estuvieron presentes en los nidos durante el 77% del día en nidos ubicados bajo arbustos y durante el 81% del día en nidos ubicados en arbustos o encima de éstos, y las hembras contribuyeron la mayor parte del tiempo dedicado a atender los nidos. Sin embargo, durante el mediodía, cuando los requerimientos evaporativos de agua estimados a partir de perfiles de temperatura de nidos artificiales fueron 10 a 15 veces mayores que durante la parte inicial de la mañana, los machos y las hembras compartieron las tareas de incubación casi por igual. Proponemos la hipótesis de que *A. alaudipes* prefiere ubicar los nidos en lugares expuestos para reducir el riesgo de depredación de los padres, pero a medida que transcurre la estación, los individuos seleccionan sitios para nidificar con mayor cobertura en la base de arbustos o dentro de éstos, debido a que el ambiente térmico los obliga a hacerlo.

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INTRODUCTION

With potentially significant fitness consequences, nest site selection is a behavior likely to be optimized by natural selection. Nest placement determines the microclimate for incubation as well as the risk of predation on eggs and incubating parents, two functions that may be in conflict, especially in extreme environments (Drent 1975, Hansell and Deeming 2002). Predation is the main source of nest failure in birds, during both egg and nestling phases (Skutch 1949, Ricklefs 1969, Martin 1995) and may present an important risk of mortality for incubating adults too (Conway and Martin 2000, Amat and Masero 2004). Especially for birds with a relatively long lifespan, a small increase in adult mortality can have major consequences for lifetime reproductive output. Therefore, individuals who choose nest sites with low risk of predation to either nest contents or themselves as incubating parents (which may be positively or negatively correlated; Martin and Roper 1988, Wiebe and Martin 1998) should be favored by natural selection. However, it may be necessary to trade off low predation risk against the need for appropriate thermal conditions, especially in hot deserts or other extreme environments.

During the early stages of offspring development, parents must regulate the microclimate in the nest because developing embryos are unable to manage their own temperatures. In nature, most species maintain eggs at temperatures (T_{egg}) around 32–35°C, irrespective of environment, incubation strategy, or body size (Webb 1987, Williams 1996). When T_{egg} drops below 25–27°C, embryonic development stops, although short periods of chilling are often not harmful for the embryo (Webb 1987, Williams 1996, Olson et al. 2006). Upper lethal T_{egg} is around 43–44°C, and embryos quickly die when this limit is surpassed (Webb 1987, Williams 1996). As a consequence, birds living in hot climates often must protect their eggs against overheating; lethal limits of their embryos do not differ from those of species breeding in cooler conditions (Grant 1982, Williams 1996, Carey 2002).

Birds breeding in desert environments must meet embryonic thermal requirements in the face of their own physiological challenges shaped by the conflicting demands of high ambient temperatures (T_a) and low water availability. When desert birds do not breed, they spend a significant part of the day inactive and in the shade to minimize risk of both overheating and water loss (Tieleman and Williams 2002). During breeding, similar behavioral adaptations are possible through biparental incubation strategies, which allow each parent to shuttle between the nest and shade, thus providing each individual with a means for behavioral thermoregulation while keeping the eggs protected from overheating. On the nest, the physiological solution for the conflict between maintaining water balance and preventing overheating depends on the gradient between body temperature (T_b) and T_a. When T_b exceeds T_a, heat can be dissipated by nonevaporative means (conduction, convection, radiation), but when the gradient between T_b and T_a becomes small, evaporative water loss is required to dispel metabolic heat production. Tolerance of increased T_b and reduced metabolic heat production could lower evaporative water loss, but these adjustments have clear limitations, and many birds are forced to cool themselves evaporatively (Tieleman and Williams 1999, Carey 2002, Williams and Tieleman 2005). The need for evaporative cooling becomes even more pressing when T_a exceeds T_b, and evaporation is the only means to cool.

We hypothesized that birds in hot deserts trade off microclimate and risk of predation when selecting nest sites, and that the optimal nest site changes as the season progresses and temperatures increase. Hoopoe Larks (*Alaemon alaudipes*) in the Arabian Desert provide a unique system to study this tradeoff between thermoregulation and predation risk because the variation in their nest sites is large, nest predation is high (Tieleman et al. 2004), and their desert environment is harsh (Tieleman and Williams 2002, Tieleman et al. 2003). In addition, the increasingly high temperatures through the course of the season provide natural variation in thermal challenges to which the larks have to respond when selecting nest sites. We examined nest site selection by Hoopoe Larks and how it changed through the season. To quantify the effect of nest site on nest predation risk, we combined the monitoring of natural nests with an experiment using artificial nests placed in different microsites. Using copper models and eggs with implanted thermocouples, we measured the thermal environment experienced by parents and eggs. Lastly, we evaluated incubation behavior of parent larks with nests in different microsites and estimated consequences for their water and heat balance.

METHODS

STUDY AREA AND SPECIES

Mahazat as-Sayd is a 2244 km^2 reserve in central west Saudi Arabia (N22°, E41°) that receives on average 90 ± 70 mm (SD) mm rain per year. The area consists mainly of flat gravel plains with grasses (e.g., *Panicum, Stipagrostis,* and *Lasurius* spp.) and small bushes (e.g., *Salsola* and *Indigofera* spp.) intersected by wadis with *Acacia* trees. Our core study area consisted of a 10 × 15 km plot in the central-eastern part of Mahazat, where Hoopoe Lark densities were relatively high, and a large proportion of the population was color banded.

Hoopoe Larks are resident in Mahazat as-Sayd. Male Hoopoe Larks are larger than females and have darker coloration on their faces. In addition, individuals have different patterns of black and white coloring on their wings. The birds breed from February to June if rainfall has been sufficient (Tieleman 2005). Rainfall in the winter before our study season, spring 2001, was adequate, and all territorial birds (approximately 75 pairs) observed in this study attempted to breed (Tieleman 2005).

NESTS

Female Hoopoe Larks build open-cup nests in three distinct microsites: on the gravel plain away from vegetation (gravel nests), on the ground at the base of small bushes (base nests), and above ground in or on top of bushes (bush nests). In our study area, they prefer *Salsola* bushes for nesting. Nests are constructed in dug-out cups when on the ground or with bases of twigs when in bushes, and lined with soft plant material. Average clutch size during the 2001 season was 3.0 ± 0.6 (SD, $n = 52$). Males and females share incubation duties. After 12–13 days of incubation, chicks hatch and remain in the nest for another 10–12 days before fledging.

We located nests in the study area by following territorial birds back to them noting the nests' GPS coordinates. Using this strategy, Hoopoe Lark nests are difficult to miss, because parents cannot afford to leave them unattended and exposed to the sun for long. Therefore, the sample of nests found was representative of nests initiated in the study area, as confirmed by the extensive coverage of the area with known nests in all neighboring territories (an estimated 90–100% of all territories in the study areas). Of all nests found ($n = 80$), 42% were being built, 55% had eggs, and 3% had nestlings at their time of discovery. Upon finding a nest, we described it by measuring compass orientation with respect to the shade provided by the vegetation (°), height above the ground (cm), diameter of the nest bush (cm) and nest cover (%). Nest cover was estimated as the average of the percentage cover from above and the percentage cover around the nest. To estimate percentage cover from above, we imagined a circle of the size of the nest touching the nest rim and estimated how much of this circle was covered by vegetation. To estimate cover around the nest, we imagined a 15 cm high ring, recorded the range of azimuths where vegetation more than 15 cm high was present, and divided this range by 360 to give the percentage cover around the nest. Cover from above and from around were correlated ($r = 0.7$, $n = 81$, $P < 0.01$) and did not differ significantly from each other ($t = 0.8$, $n = 81$, $P = 0.94$). We checked nest contents every 2.6 ± 1.4 days (SD, $n = 26$) from a distance of 5–10 m, rather than walking up to the nest.

We performed a nest predation experiment with artificial nests similar in size to real Hoopoe Lark nests, made of shallow plastic cups lined with fine grasses and containing eggs of the Sand Partridge (*Ammoperdix heyi heyi*). To minimize human odor associated with artificial nests, we left them outdoors for several days after constructing them. The artificial nests were placed in groups consisting of one gravel, one base, and one bush nest, at least 50 m apart from each other. The groups were spaced at intervals of at least 500 m. We then left the nests for predators to find. We repeated this artificial nest predation experiment three times during the breeding season, at different sites within our study area, with starting dates of 5 April ($n = 58$), 16 April ($n = 58$), and 6 May ($n = 58$). We checked artificial nests each day between the hours of 16:30 and 18:30, until they were depredated.

MICROCLIMATE

During April and May 2001, we measured air temperature (T_a), soil surface temperature (T_s), operative temperature (T_e), and egg temperature (T_{egg_unatt}) in our core study area. Wind speed was not measured. We measured T_a 10 cm above the soil surface with a 36-gauge thermocouple surrounded by a cone of aluminum foil to provide shade and to shield it from radiation. Soil surface temperature was estimated using a 36-gauge thermocouple attached to a 5×5 cm square of steel wire mesh covered with 1 mm of sand. Operative temperature is the temperature experienced by an animal without physiological thermoregulation (Bakken 1976). We measured T_e using 36-gauge thermocouples inside two copper models covered with the skin and plumage of Hoopoe Larks (Bakken 1976). Because shrikes (*Lanius spp.*) destroyed them initially, we placed our models in a cage with approximately 4 cm^2 wire mesh. We fitted three Sand Partridge eggs with 40-gauge thermocouples placed near the top of each egg to measure T_{egg_unatt}, defined as the temperature experienced by an egg without incubation by its parents. We assumed that 44°C was the lethal temperature for eggs. Copper models and eggs with thermocouples were rotated over three artificially constructed nests: one on the gravel plain away from vegetation, one at the base of a *Salsola* bush with northeast exposure (i.e., the common direction of nest placement), and one in a 30 cm high *Salsola* bush. Rotation of models and eggs ensured that differences between locations did not result from systematic temperature differences between models and eggs. A data-logger (21X, Campbell Scientific, Logan, UT) recorded the output of thermocouples every minute and stored averages over 15-min intervals.

INCUBATION BEHAVIOR

During the period 29 March–27 May 2001, we observed the incubation behavior of parents with base nests ($n = 5$) and bush nests ($n = 6$). The observer sat 50–100 m from the nest, on the ground or in a car, and using a telescope, recorded who attended the nest (male, female, unknown, or none) during the entire day (06:00–18:30). Sex was distinguished on the basis of plumage in combination with male singing and display behavior.

STATISTICAL ANALYSES

We used regression and general linear model procedures in SPSS 12.0 (SPSS Institute 2003) for statistical analyses. Proportions were arcsine-square root transformed before analyses (Zar 1996). Values reported are means ± SD.

Nest predation data were analyzed with the Nest Survival module in program MARK 4.3 (White and Burnham 1999, Rotella 2005), which allows modeling of daily survival rate as a function of continuous and categorical variables (Dinsmore

et al. 2002, Rotella et al. 2004). Dates for natural nests were scaled so that the first nest was found on day one. Nest mortality was defined as loss of all eggs in a nest. Nest success was defined as hatching of one or more eggs in the nest. Three nests that were abandoned during incubation were excluded from analysis. Data on nest site and nest cover were included as individual covariates in the MARK input file. Our first model was a basic model of constant daily survival rate for all nests. We then explored the a priori hypothesized effects of date, nest site, and nest cover, and the combined effects of date and nest site and date and nest cover. We used a sin link function for the constant survival model (which gave identical results as a logit function in this case) and a logit link function for the models including individual covariates. Models were assessed using Akaike's information criterion for small sample sizes (AIC_c) and sorted by ΔAIC_c, the difference between the AIC_c value for a given model and the top model.

The analysis for artificial nests was performed in the same fashion, except that here, the start of each experiment was defined as day 1, and date was incorporated only into the individual covariate "period". These periods were treated identically to the way we treated nest site. For both natural and artificial nests, estimates of constant daily survival rate were derived from the basic model, and estimates of nest site–specific daily survival rates were derived from the model that considered a nest site effect.

RESULTS

NEST SITE SELECTION

The number of Hoopoe Lark nests that we found increased from March to late April and early May and then declined (Fig. 1). Early in the breeding season, larks built gravel nests (i.e., on the gravel plain, 30% of total number of nests at this time) or base nests (i.e., at the base of small bushes, 40% of all nests at this time). As the season progressed, nest site preference shifted to aboveground bush nests (77% of all nests at this time; Fig. 1). Nest cover, in general, was low, but increased from 5% to 21% through the course of the season ($r^2 = 0.07$, $F_{1,92} = 7.0$, $P = 0.009$; Fig. 2A). The short, thick, fleshy leaves of *Salsola* bushes do not grow larger as the season progresses, and most of the cover was provided by the branches. The height of nests above the ground also increased through the season (Fig. 2B), not only because more larks preferred to nest in bushes, but also because they selected larger bushes (all nests: $r^2 = 0.11$, $F_{1,94} = 11.7$, $P < 0.001$; only nests in bushes: $r^2 = 0.09$, $F_{1,54} = 6.6$, $P = 0.01$). The effectiveness of nest cover is partly dependent on the orientation of the nest with respect to the shade-providing vegetation. Base or bush nests with a clear orientation (i.e., not in the center of a bush; $n = 56$) were mostly placed on the northeast (48%) or east (38%) side, and few had north (6%), southeast (6%) or northwest (2%) exposures.

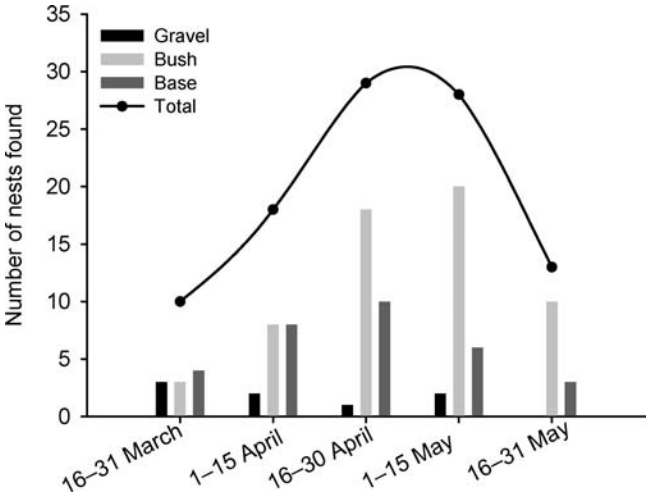

FIGURE 1. Nest site preference of Hoopoe Larks changed over the course of the breeding season, 2001, in Mahazat as-Sayd, Saudi Arabia. Hoopoe Larks built nests on three distinct microsites: on the gravel plain away from vegetation (gravel nests), at the base of (base nests) or aboveground in bushes (bush nests).

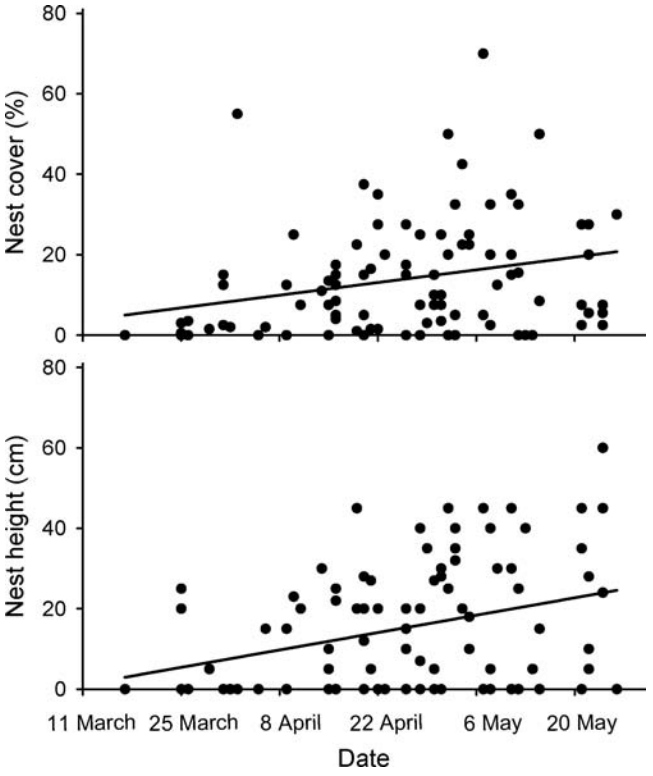

FIGURE 2. Both (A) percent cover by vegetation and (B) height of Hoopoe Lark nests increased over the breeding season, 2001, in Mahazat as-Sayd, Saudi Arabia.

TABLE 1. Daily survival rate (DSR ± SE) of natural and artificial Hoopoe Lark nests (n = number of nests) in Mahazat as-Sayd, Saudi Arabia in 2001. Estimates for all nests combined were made with the basic model. Estimates for each nest site were made with the model that included nest site. Values for natural nests are averages over the entire breeding season; values for artificial nests are averages over the three time periods in April and May during which we conducted the experiment.

Nest site	DSR natural nests	n	DSR artificial nests	n
Gravel	0.870 ± 0.070	4	0.585 ± 0.043	58
Base	0.819 ± 0.039	22	0.611 ± 0.041	58
Bush	0.820 ± 0.032	31	0.597 ± 0.042	58
All nests combined	0.824 ± 0.024	57	0.598 ± 0.024	174

NEST PREDATION

We monitored 57 natural nests and found daily survival rates between 0.819 and 0.870 for different nest sites, with the highest values for gravel nests (Table 1). We found no evidence for effects of date, nest cover, or nest site on daily survival rate, since no model had better support than the basic, constant daily survival rate model (Table 2).

Daily survival rate of artificial nests in different microsites varied between 0.59 and 0.61 (Table 1). We found no evidence that nest site or period during the season affected the chance that an artificial nest was depredated (Table 3).

NEST MICROCLIMATE

From the beginning of April until the end of May 2001, average daytime (06:00–19:00) T_a increased from 28.2°C to 38.8°C, and T_s from 29.8°C to 50.8°C, while maximum T_a increased from 34.6°C to 47.6°C, and maximum T_s from 45.5°C to 67.1°C. Daily variation in T_a and T_s has been described elsewhere (Tieleman and Williams 2002).

Average daytime (06:00–19:00) T_e measured with copper models on the gravel plain increased from 35.4°C to 42.1°C between early April and late May. The daily patterns of T_e over the course of the season revealed not only higher but also broader peaks later in the season (Fig. 3A–C). Parents on gravel nests experienced the hottest conditions, and although maximum T_e at base and bush nests was similar, parents on base nests experienced up to 5°C higher T_e during a portion of the day compared with those on bush nests (Fig. 3B–C). The difference between gravel nests and base and bush nests became smaller as the season progressed (Fig. 3A–C). Between early April and late May, average daytime T_{egg_unatt} of unattended artificial nests increased from 30.0°C to 46.4°C (gravel nests), 28.5°C to 40.5°C (base nests), and 28.6°C to 43.1°C (bush nests). Maximum values increased from 41.1°C to 59.2°C (gravel nests), 35.3°C to 49.3°C (base nests), and 37.3°C to 54.8°C (bush nests). Daily patterns showed that T_{egg_unatt} in gravel nests was always higher than in base or bush nests (Fig. 3D–F). Early in the season, T_{egg_unatt} was similar in base and bush nests and remained below 44°C throughout the day. Later in the season, eggs in bush nests reached temperatures exceeding those in base nests by up to 9°C, thereby resembling gravel nests and surpassing the lethal limit for eggs for up to 7 hours per day (Fig. 3). The number of hours that T_{egg_unatt} exceeded 44°C increased over the course of the season at all three nest sites (Fig. 4) and was significantly higher in gravel nests than in bush nests, but not significantly different between bush and base nests (effect test for date: $F_{1,76} = 11.0$, $P = 0.001$; nest-site: $F_{2,76} = 40.0$, $P < 0.001$; post-hoc analysis using contrast type "repeated": gravel vs. bush nests $P < 0.001$, bush vs. base nests $P = 0.23$).

TABLE 2. Summary of model selection results for daily survival rates of natural nests of Hoopoe Larks in Mahazat as-Sayd, Saudi Arabia, during the breeding season of 2001. Models are ordered by Akaike's information criterion corrected for small sample size (AIC_c). K is the number of parameters, ΔAIC_c is the difference in AIC_c values from that of the top model, and w_i is the model weight.

Model[a]	K	Deviance	ΔAIC_c	w_i
Constant	1	147.61	0.00	0.43
Date	2	146.88	1.32	0.23
Cover	2	147.60	2.03	0.16
Date + cover	3	146.86	3.35	0.08
Nest site	3	147.21	3.70	0.07
Date + nest site	4	146.58	5.14	0.03

[a] AIC_c of top model = 149.62.

TABLE 3. Summary of model selection results for daily survival rates of artificial nests in Mahazat as-Sayd, Saudi Arabia during spring 2001. Models are ordered by Akaike's information criterion corrected for small sample size (AIC_c). K is the number of parameters, ΔAIC_c is the difference in AIC_c values from that of the top model, and w_i is the model weight.

Model[a]	K	Deviance	ΔAIC_c	w_i
Constant	1	536.26	0.00	0.53
Period	2	533.10	0.89	0.34
Nest site	3	536.07	3.86	0.08
Period + nest site	5	532.82	4.70	0.05

[a] AIC_c of top model = 538.27.

INCUBATION RHYTHMS

Total nest attendance averaged 77 ± 5% ($n = 5$) of total daylight time for base nests and 81 ± 7% ($n = 6$) for bush nests. We tested for differences between nest sites, taking into account average T_a on the observation day as covariate, but found no significant effect of nest site or T_a on total nest attendance (effect test for nest-site: $F_{1,8} = 0.5$, $P = 0.48$; T_a: $F_{1,8} = 0.2$, $P = 0.65$). The fraction of total nest attendance contributed by the female was 65 ±7% ($n = 5$) for base nests and 74 ± 9% ($n = 6$) for bush nests (effect test for nest-site: $F_{1,8} = 1.2$, $P = 0.31$; T_a: $F_{1,8} = 1.2$, $P = 0.31$). Inspection of the daily pattern of attendance, for base and bush nests

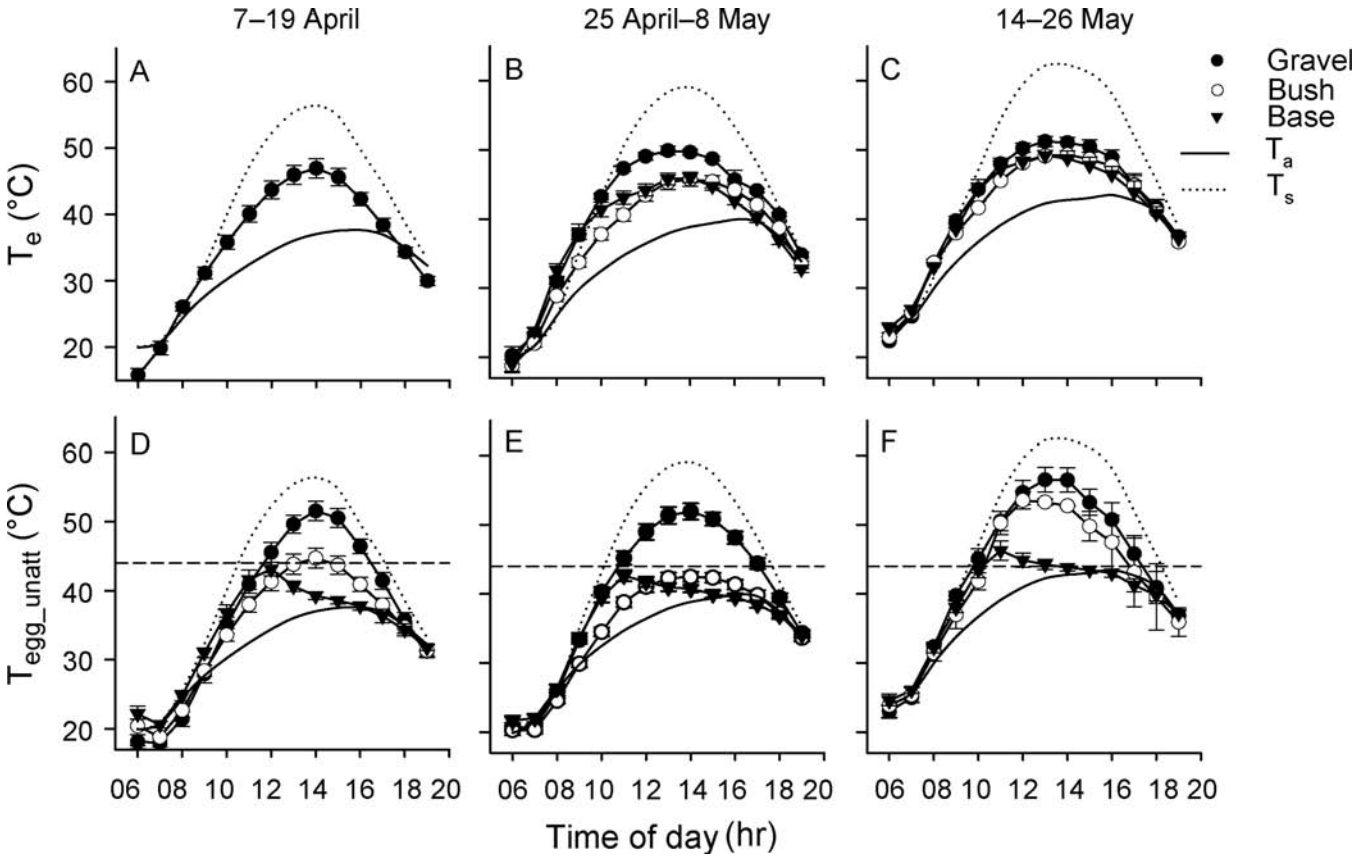

FIGURE 3. Daily patterns of operative (T_e, ± SE) and egg (T_{egg_unatt}, ± SE) temperature in unattended artificial Hoopoe Lark nests on the gravel plain, at the base of bushes, and above ground in bushes in Mahazat as-Sayd, Saudi Arabia. Results were averaged over 12-day periods in mid-April (A, D), late April to early May (B, E) and the second part of May (C, F), 2001. Solid lines depict average air temperature, and dotted lines depict average soil temperature. Horizontal dashed lines reflect assumed lethal $T_{egg} = 44°C$.

combined, showed that attendance by males was higher in the middle part of the day than early in the morning and late in the afternoon (effect test for time period: $F_{2,30} = 20.2$, $P < 0.001$), whereas attendance by females did not differ throughout the day (effect test for time period: $F_{2,30} = 0.8$, $P = 0.45$; Fig. 5).

DISCUSSION

Despite breeding under hot and dry conditions, Hoopoe Larks selected nest sites remarkably exposed to solar radiation during large parts of the day instead of choosing thermally favorable shaded locations that were also available in their territories. During the course of the breeding season, as temperatures and solar radiation increased, nest site preference shifted from open gravel plains and the bases of bushes to nests aboveground in or on top of increasingly higher bushes and with slightly more cover. Considering that many passerine species build their nests in dense vegetation or holes with complete shade, regardless of the nest site selected, nest cover was low for Hoopoe Lark nests. Nest site selection did not appear to be influenced by risk of predation on eggs; nest predation at all microsites was high, with only a weak trend suggesting that nests on the gravel plain away from vegetation had a lower risk of nest predation. We suggest that predation risk for incubating adults may be lower when they can view their surroundings (Amat and Masero 2004). This factor may overrule other considerations, explaining the preference for exposed nest sites, despite poor thermal conditions and high risk of losing the nest to predation.

Whereas incubating adults may experience lower predation risk in more exposed nests, nest contents are often at lower risk of predation in more concealed nests (Martin and Roper 1988, Martin and Li 1992). However, assessment of nest predation risk, a skill attributed to some passerines (Fontaine and Martin 2006), may be difficult for Hoopoe Lark parents because the diversity of predators (including reptiles, birds and mammals) is high, and nest predation can vary significantly from year to year in Mahazat as-Sayd. In 2001, most nests did not survive to fledging, whereas in 1998, most nests did produce fledglings, and many territories housed

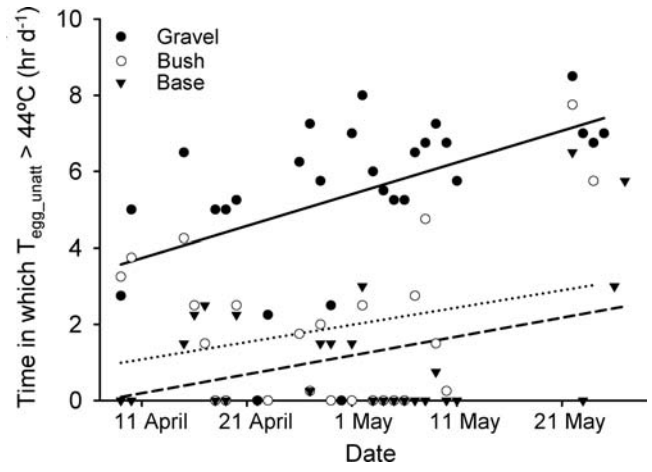

FIGURE 4. The number of hours per day that egg temperature (T_{egg_unatt}) exceeded the assumed lethal limit of 44°C in artificial unattended gravel nests, base nests and bush nests of Hoopoe Larks increased with calendar date in Mahazat as-Sayd, Saudi Arabia, in 2001.

complete Hoopoe Lark families after the breeding season. In addition, the daily survival rate of artificial nests during 2001 was 0.598 (Table 1), but an identical experiment in 1999 yielded a higher daily survival rate of 0.903 ± 0.014 (SE, $n = 50$; BIT, unpubl. data). These observations suggest that the predator assemblage and abundance differ among years, providing a temporally variable selective force that does not uniformly favor one type of nest site over others.

Whereas the rate of predation on eggs likely varies with year, thermal conditions are more predictable and therefore provide a more uniform selection regime. The thermal environment in the nest can be evaluated from two perspectives:

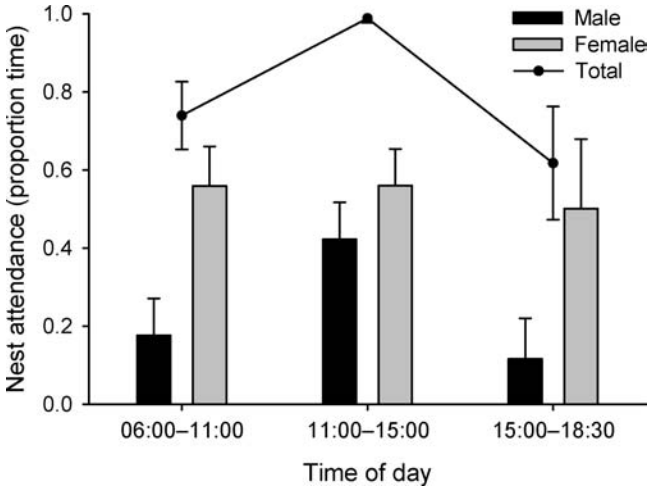

FIGURE 5. Proportion of time (± SD) spent on the nest by female and male Hoopoe Larks during three different periods of the day during the breeding season, 2001. Connected dots depict total nest attendance (± SD).

the conditions experienced by the eggs, which determine the time required for parental attendance to prevent overheating of the clutch, and the conditions experienced by the incubating parent, which affect water loss and energy expenditure required to maintain heat balance. From both perspectives, gravel nests are unfavorable. Egg temperatures exceed lethal limits for longer time periods than base or bush nests; gravel nests therefore demand longer time periods of protection by an attending parent. In addition, T_e experienced by the incubating parent is higher, resulting in increased water requirements for evaporative cooling to the parent. Base nests provide the most favorable environment for eggs, minimizing time demands on parents, but bush nests provide the most attractive situation from a parental thermoregulatory perspective, presumably counteracting the slightly higher attendance demands later in the season. The increase in nest height over the course of the season suggests that opportunities for parental thermoregulation play an increasingly important role when environmental conditions become more challenging. Higher bushes may provide more shade and certainly allow better access to wind, facilitating convective cooling. The difference in T_e between base and bush nest sites may be underestimated with the copper models, which do not include the effects of postural adjustments such as ptiloerection and the holding of wings away from the body, as commonly displayed by a Hoopoe Lark perched on its nest aboveground in a bush. When T_a becomes too high, a Hoopoe Lark no longer perches over its nest like a parasol, but presses down on its eggs, presumably creating a thermal gradient to allow heat transfer from the egg to it, the parent, in order to maintain T_{egg} below lethal limits. Studies continuously monitoring both T_{egg} and parental T_b in a hot, dry environment do not exist, but a study on Mourning Doves (*Zenaida macroura*) in the Sonoran Desert found that incubating birds maintain T_b below T_{egg} to allow heat loss from the egg (Walsberg and Voss-Roberts 1983). In addition, among captive Ringed Turtle-Doves (*Streptopelia risoria*) breeding in an environmental chamber kept at 45–46°C, the incubating member of a pair had 0.3°–1.9°C lower T_b than the nonincubating partner (Walsberg and Voss-Roberts 1983). The difference in T_b was attributed to more frequent panting by the incubating parent than by the nonincubating one, presumably entailing substantial increases in evaporative water loss. How free-living birds such as Hoopoe Larks living in hot environments without access to drinking water simultaneously manage water balance and T_b during incubation remains to be studied.

Detailed information about the simultaneous effects of temperature, wind, and radiation on heat exchange of free-living birds in hot environments is rare (Dawson and O'Connor 1996). Consequently, estimation of thermoregulatory costs must rely on extrapolating laboratory measurements to field conditions. We used data on total evaporative water loss (TEWL) of Hoopoe Larks, measured between 0 and 50°C in the laboratory (Tieleman et al. 2002), to translate

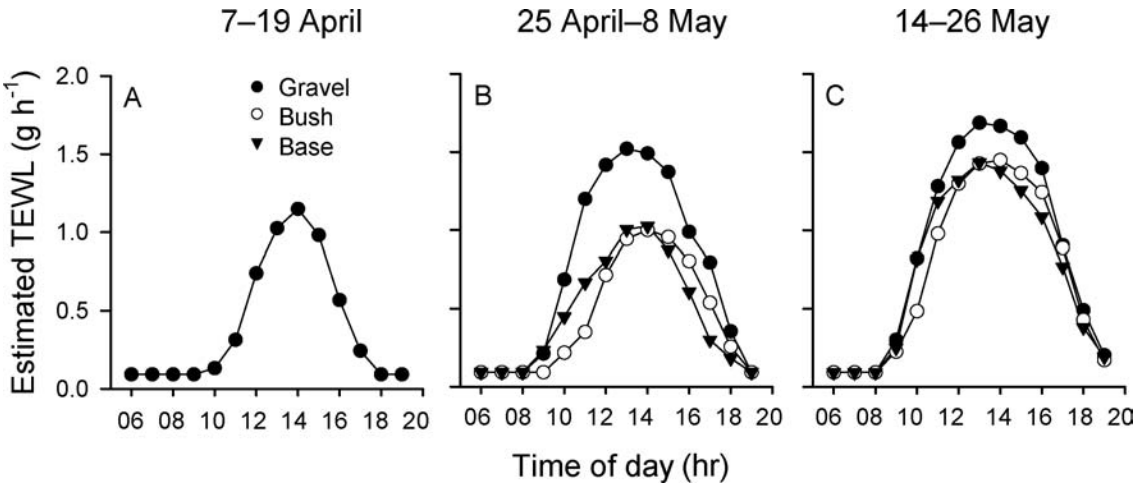

FIGURE 6. Estimated total evaporative water loss (TEWL, g h^{-1}) of incubating Hoopoe Larks based on operative temperature (Fig. 3A–C) and laboratory measurements of TEWL (Tieleman et al. 2002), for gravel, base and bush nests in three different periods of the breeding season, 2001, in Mahazat as-Sayd, Saudi Arabia.

T_e (Fig. 3A–C) to TEWL costs of incubation at the different nest sites (Fig. 6A–C). When we compared patterns of T_e and estimated TEWL, most striking were the large consequences for water loss with only small shifts in T_e. The 10–15 fold increase in TEWL between the early morning hours and the middle part of the day highlighted the importance of the role of the male during incubation. Whereas his share of total nest attendance was small early and late in the day, during the costly—in terms of water—time in the middle part of the day, his attendance was almost identical to the female's. During the nestling phase, the contributions of male and female to brooding and feeding the chicks were almost identical and result in similar water influx rates as measured with doubly labeled water (Tieleman et al. 2003).

With small clutch size, some years without reproduction, low metabolic rate, and probably high annual survival rates (Tieleman 2005), Hoopoe larks can be included in the category of relatively long-lived birds that should avoid even small increases in risk of mortality, because they have large consequences for lifetime reproductive output (Martin 1993, Ghalambor and Martin 2001). The relative fitness value of a single clutch is small compared with even a slight change in adult annual survival. The preference for exposed nest sites in Hoopoe larks may well be explained by a decision matrix in which adult survival is the main selective factor, and thermal conditions and nest predation are secondary considerations. Experiments altering nest exposure and measuring predation risk for incubating parents of long-lived bird species could shed light on this hypothesis.

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